Evolution in methods of pollination.

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[*Concluded from p. 46.*]

Among animals, the phase of natural selection known as sexual selection comes to the front in the production of many things which we call beautiful or curious, such as the gorgeous colors of male birds and butterflies, the horns of beetles and reindeer, the tusks of boars and elephants, the chirping of crickets and the songs of birds. (It is noteworthy, here as elsewhere, how similar organs have been independently developed for similar ends in most widely different classes of organisms.) The higher plants, however, because of their fixed position, are removed from the power and influence of sexual selection, and its offices of the production of attractive qualities are performed for them in a most remarkable way by the agency of insects. Insect selection takes the place of natural selection, and to it we largely owe the fragrance, color and form of our beautiful flowers.[1] This is one side of the picture; the animals themselves are the other. Side by side with the flowers they frequent they have themselves been changed, their proboscides lengthening with the flower tubes, their bodies becoming better adapted to the forms of the blossoms and to the carrying of the pollen, their wits sharpened to find the means of getting at the hidden honey with the least possible loss of time and strength, and to read quickly the posters hung out by the plants, which enable the more intelligent customers to distinguish one kind of flower from another, and show them when the time for visiting is reached or passed. So now, instead of the primeval cockroach-like creatures, there are insects as varied and wonderful in form and structure as the flowers they frequent.

This subject is full of interest, and since the time of Darwin has been widely studied, but the knowledge accumulated should be put into form convenient for every day use. If, as we believe, flowers have been produced by a gradual adapta-

[1] The variations — the presuppositions of progress — are, of course, inherent in the plant nature, produced by causes not yet fully understood. The insects have simply chosen and therefore perpetuated those best adapted to their own needs which must also of necessity be those which are advantageous or at least not injurious, to the plants themselves.

tion to the reciprocal wants of plants and their visitors, from fructifications essentially like the spore-bearing spikes of the heterosporous Equisetums of which geologists write, this ought to be known by every student, and everyone should be able to see from the manual that, in each order, the method of fertilization is to a certain extent an index of the degree of specialization of the reproductive apparatus, the most important part of the plant. In many orders there is a most beautiful transition from anemophilous (usually polygamous, monœcious or diœcious) species through almost exclusively self-fertilized hemaphrodite ones to those that are incapable of self-fertilization. For example, in the Ranunculaceae, in the gradation from the wind-blown inflorescences of polygamous Thalictrums to the inconspicuous, almost exclusively self-fertilized flowers of Myosurus minimus; from this to the genus Ranunculus (whose small-flowered species, such as R. abortivus and R. sceleratus closely resemble Myosurus in the arrangement of the carpels and stamens, while the large species, R. repens, R. bulbosus, etc., are abundantly visited and crossed); from Ranunculus to Aquilegia, and from Aquilegia to Delphinium and Aconitum, there is a suggestion in the compass of a single order of the probable historical development of irregular, brightly colored, greatly specialized, insect-fertilized forms from the grass-like or pine-like, spore-bearing stalks of the ancestors of our dicotyledons.

At a certain stage of development, these changing plants will be perfectly adapted to neither wind nor insect fertilization; then those individuals whose stamens and pistils are borne in adjacent clusters, or better yet, within the same bracts, will be most sure of ripening seed. Clavaud says: "There does not exist a diœcious plant which cannot exceptionally offer the two sexes upon the same stalk." The common occurrence of stamens in the pistillate, and of pistils in the staminate clusters of trees and other plants described as monœcious or diœcious, is known to every observer. Such variations, sometimes perhaps preserving the lives of the plants which possess them, will be passed on to their descendants. In other words, hermaphrodite flowers may have arisen from unisexual ones, as unisexual ones are now actually being produced from hermaphrodite (e. g. in many genera of Labiatæ, in some species of Silene). So it comes to pass that though the majority of wind-fertilized plants have the sexes

separated, almost all entomophilous ones have stamens and pistils in the same flowers. Müller therefore considers diclinism to have been the original condition of phanerogams, from which hermaphroditism has been developed by natural selection. Darwin takes exactly the opposite view. But it hardly seems necessary to adopt either exclusively, for both hermaphrodite and unisexual forms are common among the lower plants. Why cannot both forms have been transmitted from the pteridophyte-like ancestors of phanerogams? Diclinism and bisexualism may be collateral branches, one not necessarily older than the other, though in many individual cases it is evident that one has been, or is being derived from the other.

When a plant has become adapted either to self or insect fertilization there is no longer necessity for the production of vastly greater quantities of pollen than can be used, for either method is more sure than dependence upon wind agency. Frugal nature then turns the energy no longer needed for spore formation into another channel. Some of the stamens, losing their power to produce pollen, may become exclusively organs of attraction. Numerous transition stages are represented in the genera Thalictrum, Clematis, Nymphaea, etc. The origin of brighter color may be like that of nectar (BOTANICAL GAZETTE, vol. XV, p. 177) a result of the unusually active life processes in connection with the strong current necessary to supply the ovules and anthers with materials required for the development of their richly fed spores. The same principle is at work which Wallace and others have shown to prevail among animals, whose highly colored organs are, as a rule, those which are most continually exercised; e. g. the wings of butterflies, the wings, tails and beaks of birds, etc.

Again, the rule that among animals a great number of similar segments is a mark of low organization, seems to hold good here. Contrast the numerous stamens and pistils and the variable number of petals or sepals of water lilies, buttercups and anemones with the small and always constant number characteristic of the aristocratic families, the Violaceæ, Compositæ, Labiatæ and Scrophulariaceæ. This decrease in the number of the floral organs is often accompanied by further specialization by the union of their individual members to secure still better protection of the pollen, honey and ovules and better adaptation to the agents of pollination.

When cross-fertilization by means of insects has become assured, the color, time of flowering, fragrance, the length of the corolla tube, the form and position of the petals and sepals, all have reference to time of flight and character of the especially invited guests. Every hair has a meaning. Every curve is an adaptation. The power of self-fertilization, at first indispensable, may become useless. A struggle for existence arises between the two methods and the least efficient goes to the ground. So cross-fertilization is, as a rule, alone possible among the majority of orchids, some Compositæ, some species of Salvia, Aconitum, Corydalis, Dianthus, Malva and others. Many changes, progressive and retrogressive, are still going on. It is known that the honey of more than one hundred and thirty-two flowers can be plundered from outside without the touching of the stamens or stigma. In these cases at least, perfection has, not been reached; but the wonderful contrivances to prevent the entrance of useless guests, such as hairs on the calyx, corolla or stamens, slipperiness of the corolla, a pendent position of its tube, or the accumulation in the petals of matters offensive to insects, show that some species are on the high-road to it.

So much for flowers; but there are weeds, hundreds of them, widespread and homely. Many, perhaps all, of those which have the rudiments of calyx and corolla are degraded forms, descendents of species once fertilized by insects, but which, because of the extinction of the particular ones on which they either depend, or because they have spread into regions where these insects are not, or because thrown into the shade by the superior attractions of their neighbors, have been obliged to resort again to wind agency (Plantago?), or to adapt themselves to almost exclusive self-fertilization (Veronica hederæfolia). In either case there is no longer need of attractive organs and the petals have accordingly been reduced. The evil effects of continued self-fertilization may have had a share in this result; but probably not to a great extent, for such effects will be largely counteracted by the wide dissemination so characteristic of weeds, by which these low forms are exposes to great variation of climatic conditions. The loss is then of beauty, not of strength. Change of environment seems often to have as beneficial results as cross-fertilization in the stimulation of the life processes and the production of varieties. The degradation here, as elsewhere, is only a peculiar form of adaptation.

The theory that, by whatever means gained (by the crossing of individuals if possible, if not by self-pollination), the great object of plant-life is the production of seed, the continuance of its species, receives further support by the presence in many of the forms, most beautifully adapted to the visits of insects, of cleistogamic flowers. These are minute, never-opening flowers whose stamens produce very little pollen (from 100 to 400 grains in contrast to the 243,600 of Leontodon or the 3,654,000 of Peony), but the anthers are in close contact with the stigma, none of the pollen is wasted and the inevitable self-fertilization causes the ripening of seed enough to secure the the existence of the species, if for any reason the more conspicuous flowers are not visited. Kuhn enumerates 44 genera which have flowers of this kind; Darwin adds 12 (Viola, Impatiens, Lespedeza, Specularia, Campanula Lathyrus, etc.) May it be this small form which alone survives in some degraded species?

Such study has led me to many delightful hours spent in watching the visits of insects to flowers, with, for one result, great respect for Darwin's famous aphorism, "nature abhors perpetual self-fertilization." For though I waited a long time often, sometimes for days together, to "win the secret of some weed's plain heart," the flower lover was almost sure to come at last in the form of buzzing bombuses for the two species of Monotropa, a tiny fly for the little shore pin weed (Lechea thymifolia), clumsy bugs for the honeyless, dull-colored purple trillium (Trillium erectum), pollen eating bees and flies for the homely ragweed (Ambrosia artemisiæfolia.) During the last spring, summer, and autumn I caught a thousand insects on one hundred and forty-three species of plants (one of a kind on each). One hundred and thirty-one of these flowers are visited by Hymenoptera, fifty-seven by Lepidoptera, sixty-two by Diptera, seven by the ruby-throated humming bird. I shall not soon forget the first sight of a humming bird draining dry the nectar cups of the columbine (Aquilegia Canadensis); nor the daily visits which he afterwards made to the trumpet honeysuckle, trumpet creeper, fraxinella, Petunia, Lunaria, Rhododendron, or Rhodora; nor the silent watching in the evening for the ghost-like, dusky-winged humming bird moth, whose capture is as memorable as that of a boy's first six-pound salmon; nor the dark evening when a valiant sweep of the net over the

Japanese honeysuckle captured a supposed humming bird moth which proved to be only a June bug. The beautiful clear-winged moth (Sesia), whose first visit to the Azalea of the botanic garden was so sudden and brief that after long waiting vainly for his return I almost concluded that he had been the delusion of an excited imagination, afterwards proved himself a capturable reality and we enjoyed the further acquaintance with his family through their visits to Lunaria, Hydrophyllum, Dictamnus, Syringa, and Vinca. The memory of the gorgeous red butterfly which twice visited the smooth sumach (Rhus glabra L.), eluding our nets both times never again to appear notwithstanding our patient waiting and the reward offered for his arrest, will haunt me through the winter months and until the shade of one of his descendants joins the full ranks of those who met death on the sumach field.

Botany and zoölogy at the start are one, but when the debatable ground occupied by organisms neither animal nor vegetable is passed, each has a clear country until paths cross again in this region of reciprocal plant and animal selection. If the descent theory is true, a natural system of classification which shall show true relationship is, to some extent, possible. Such a classification has been largely adopted for the lower plants, and it will come for all. Then the standard manual of botany will no longer separate what nature has joined together; the gymnosperms will not stand between the sister classes of angiosperms, nor gamopetalous between the polypetalous and apetalous exogens. The relationship which all acknowledge will be clearly shown. The arrangement of species in each order will be a story in brief of the development of the order itself, the means of fertilization being an important factor of the determination of the comparative degree of specialization of each species. Then too we shall do away with the undignified jump from phanerogams to cryptogams, using instead the natural ladder which has been stretched between them, the gymnosperms, whose life history is in some respects so like that of pteridophytes, in others so like that of close-ovaried plants that it is hard, impossible indeed, to say to which they are most closely related. Our classification will follow the teachings of geology, histology, embryology, and common sense, and, standing on the vantage ground of a manual founded on the brotherhood

of plants, we can look over the broad battlefield of biology, and see the vast territories which have been conquered, then relinquished in turn by mosses and fungi, pteridophytes, cone-bearing plants, endogens, apetalous and polypetalous exogens, and now are largely held by today's victors, the gamopetalous dicotyledons. We can see how the hardy pines have fought stubbornly for centuries, yielding ground only inch by inch to the endogens, the secret of whose final victory was that, Niobe-like, they protected their children though perishing themselves. We can see too how these children have been driven to the marshes, windswept plains, and cold mountain hills by the onslaughts of their more completely armed younger brothers, who, leagued with the great insect kingdom, are carrying all before them.

That will be a view well worth looking at and the sooner we begin the climb to the high ground, the better. The botany of the past is a most vital part of the botany of today. Zoölogy must join hands with us. We are dependent on each other. Distribution, genealogy, and environment will enter largely into the manuals of the future. Then the touch of nature which makes the whole world kin will be added to the long Latin names and mechanical descriptions.

[The foregoing paper was prepared at Mt. Holyoke Seminary and College, S. Hadley, Mass.]

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(WITH PORTRAIT.)

This rising young botanist died in New York city on Dec. 22, 1891 from an abcess on the brain. He was especially known as an independent and indefatigable worker upon our Montana flora. Gone is he, no more to roam with me our Montana plains, no more to climb these mountains, no more to sit beside me in my study gazing through my microscope to discover Nature's secrets, no more to use his skilful pencil in catching upon paper the singular beauties of plant structure; gone while we are mutually planning for many more years of service together in our beloved science; gone, adding one more to the mysteries of divine providence which so often removes those that seem nidispensable.